MAIN FISH POPULATIONS AND THEIR RELATION TO THE BENTHOS IN A SILTED BAY OF NEW CALEDONIA, AS DETERMINED BY VISUAL CENSUSES

by

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ABSTRACT. - The fish communities of St Vincent Bay (New Caledonia) and their relation to the benthos were studied by visual censuses. In all, 89 species of fish (31 families) were recorded, the major species in density and biomass being *Leiognathus rivulatus*, *Secutor ruconius*, *Lethrinus genivittatus* and *Scolopsis temporalis*. The trophic structure was dominated by macro-invertebrate feeders and plankton feeders whereas piscivores, micro-invertebrate feeders and herbivores were less important. These characteristics are common throughout most of the tropical Indo-Pacific coastal fish assemblages. Species richness of fishes was correlated with the species richness and the abundance of cnidarians whereas fish density and biomass were correlated with the species richness and the abundance of sponges and ascidians. The species structure of the ichthyofauna was also linked to two bottom characteristics, namely siltation and benthos diversity and abundance. Five fish species groups were identified: (1) species of the silted stations where benthic communities were scarce; (2) species usually seen on bare sand bottoms; (3) species occurring where benthic communities were diversified and abundant; (4) species of the "lagoonal grey bottoms"; (5) species occurring where crevices or debris were present with algae. These results support the view that some tropical Indo-Pacific trawl fisheries have declined by modifying bottom habitat rather than by excessive fishing effort.

RÉSUMÉ. - Les communautés de poissons de la baie de Saint-Vincent (Nouvelle-Calédonie) et leur liens avec les communautés benthiques ont été étudiés par comptages en plongée. Au total, 89 espèces de poissons (31 familles) ont été répertoriées, les peuplements étant dominés en densité et en biomasse par *Leiognathus rivulatus*, *Secutor ruconius*, *Lethrinus genivittatus* et *Scolopsis temporalis*. La structure trophique de l'ichtyofaune était dominée par les macro-carnivores benthiques et les planctonophages, les piscivores, les micro-carnivores benthiques et les herbivores étant moins nombreux. Ces caractéristiques sont communes à de nombreux peuplements de poissons des régions indo-pacifiques intertropicales. La richesse spécifique de l'ichtyofaune était corrélée avec le nombre d'espèces et l'abondance des cnidaires tandis que la densité et la biomasse étaient corrélées avec celle des éponges et des ascidies. L'ichtyofaune présentait une structure spécifique également liée aux caractéristiques du fond. Cette structure variait selon deux gradients, l'envasement d'une part, la diversité et l'abondance du benthos d'autre part. Cinq groupes d'espèces de poissons ont été individualisés. Le premier ensemble caractérise les stations envasées où les communautés épibenthiques étaient rares. Le second rassemble des espèces rencontrées préférentiellement sur des fonds de sable nu. Le troisième est caractéristique des stations où les communautés benthiques étaient les plus diversifiées et les plus abondantes. Le quatrième est caractéristique des "fonds gris" du lagon et le dernier ensemble des fonds où anfractuosités, débris et algues étaient présents. Ces résultats montrent l'importance des liens existant entre les peuplements ichtyologiques et la nature du fond. Ils tendent à confirmer l'hypothèse avancée de modification de la nature des fonds pour expliquer le déclin des pêcheries au chalut de la région indo-pacifique intertropicale. Cette hypothèse serait prépondérante par rapport à un effort de pêche trop important.

Key-words. - Fish community structure, ISEW, New Caledonia, Soft bottom, Fish-benthos relations.

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The soft bottom fish communities found in New Caledonia are very similar to those from Australia and South East Asia where they are heavily exploited by trawl fisheries (Kulbicki and Wantiez, 1990a; Wantiez, 1993). With increasing fishing effort, the physical action of trawls on the fishing grounds has modified the habitat (Hutchings, 1990), and shifts in species composition have taken place (Sainsbury, 1982; Hutchings, 1990; Harris and Poiner, 1991). The soft bottom fish communities are significantly linked to benthic characteristics (Dredge, 1989; Watson *et al.*, 1990; Wantiez, 1993), but these links have been little studied at a small scale from *in situ* observations in an unexploited zone. St Vincent Bay, in the South West Lagoon of New Caledonia, offers trawling grounds which have been very little affected so far by trawling and it may therefore allow the observation of soft bottom fish communities in a near pristine state (Wantiez, 1993). The aim of this study was to estimate, from visual censuses, the natural relationships between the structure of the fish community and the benthic community. In particular, the links between the trophic structure of the ichthyofauna and the benthic characteristics were studied. By implication, this study should show how modification of benthic characteristics may induce variations of soft bottom fish community structure and trophic organisation.

MATERIAL AND METHODS

Sampling

Eleven stations were chosen at random in the South Bay of St Vincent (Fig. 1). At each station, a 200 m transect line was laid. Fish were recorded by two divers, one on each side of the line. For every 10 m section of the transect line, each diver identified the species and recorded the number and the size of the fishes along with the perpendicular distance of the fish from the transect. Length was given in 2 cm classes for fish smaller than 20 cm, 5 cm classes for fish between 20 and 50 cm, and 10 cm for fish larger than 50 cm. The distance from the fish to the transect was recorded in 1 m classes up to 5 m, and in 2 m classes beyond 5 m. Fish were not recorded beyond 10 m from the transect. In the case of schools of fish, the nearest and furthest distances were recorded and fish were assumed to be evenly distributed between these two distances.

For every 10 m section of the transect line a third diver estimated the percentage of bottom type in each of 5 classes: sand, silted sand, silted sand with debris, silt, and silt with debris. The benthic organisms were recorded by the same diver according to an abundance scale of 1 to 5 (Table I), in a path 1 m wide centred on the transect. Only the largest and most conspicuous benthic organisms (size > 1 cm) were taken into account. No attempt was made to look for hidden organisms in sponges or reef formations or for buried species such as most worms, sand sea urchins or bivalves. Crustaceans were not taken into account.

Each fish species was attributed a diet having five possible components: fish, macro-invertebrate (benthic prey > 2 mm size), micro-invertebrate (benthic prey < 2 mm size), algae and plankton. A given species may have several components in its diet and so is included in several trophic categories. This procedure is more precise than the usual attribution of a species to a single trophic category (Parrish *et al.*, 1986). Wantiez and Kulbicki (1991) give a detailed account of the trophic classification of the fish encountered during the present study.
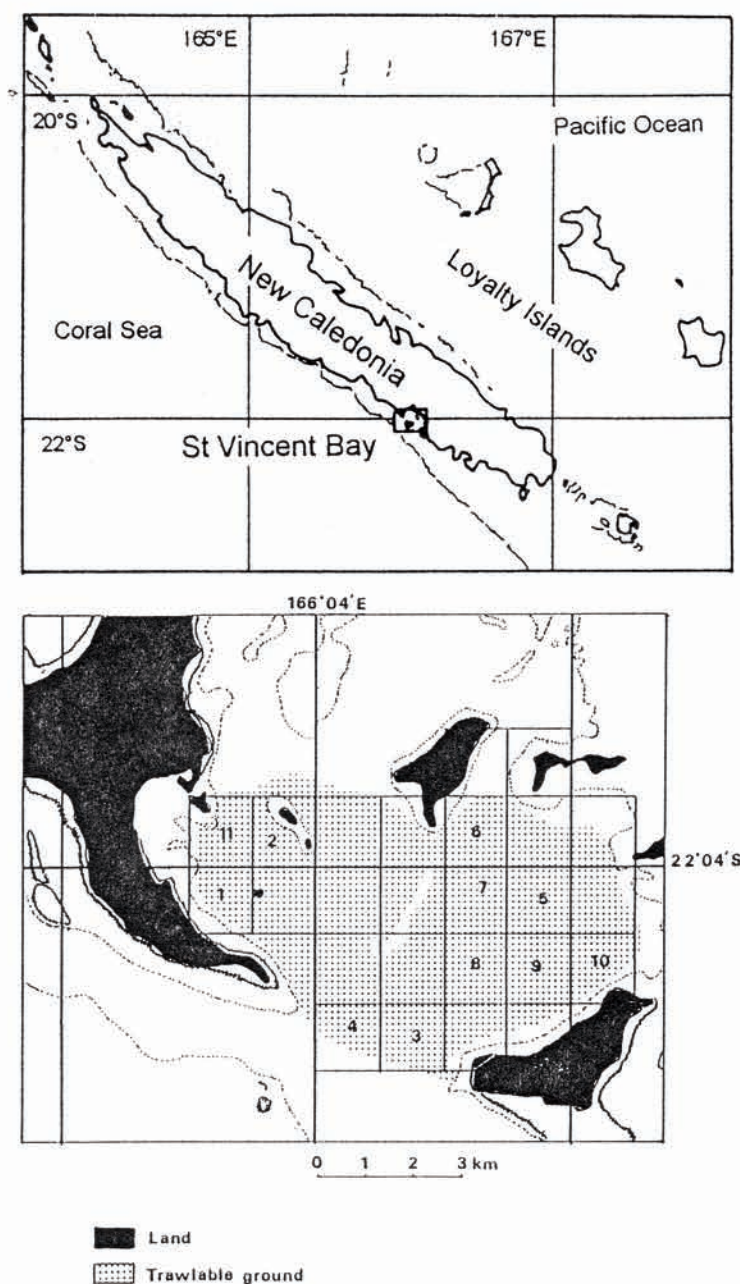
Fig. 1. - Location of the stations in St Vincent Bay, New Caledonia. The stations were chosen at random within the grid.

Analytical methods

Fish densities were calculated using the programme TRANSECT which was provided by SHARE Program Library Agency and based on the work of Burnham *et al.* (1980). Biomasses were later estimated using a modified version of TRANSECT and length-weight relationships for the species involved (Kulbicki *et al.*, 1993).

An abundance estimator was calculated for each benthos group of individual organisms at each station. Each group was attributed an abundance estimator equal to the mode of their abundance class for each 10 m section of the transect (Table I). The same abundance estimators were used for the colonial organisms (Table I). The overall abundance estimator of a benthos group at a station was calculated as the sum of the estimators for each 10 m section. This method allowed us to obtain an overall index linked to the density (Watling *et al.*, 1978). Then, Spearman rank order correlation coefficients (Siegel and Castellan, 1988) were calculated to correlate species richness, density and biomass of the entire fish population and of their various trophic groups with the main benthic groups.

Table I. - Indices used to record benthic organisms along the transect line.

Index	Abundance estimator	Abundance level	Individual organisms number / transect	Colonial organisms % of area covered
1	1	present	1	$\leq 1\%$
2	3	rare	2 - 5	$> 1 - 2\%$
3	8	scarce	6 - 10	$> 2 - 5\%$
4	30	abundant	11 - 50	$> 5 - 20\%$
5	80	very abundant	> 50	$> 20\%$

The fish species were related to the main benthic features for every 10 m section. An observed occurrence (O_{ij}) was recorded for a given species of fish (i) and for a given benthic feature (j). A theoretical occurrence (T_{ij}) was calculated for fish species i and benthic feature j assuming that fish species i is randomly distributed whatever the characteristics of the benthos:

$$T_{ij} = N_i \ P_j \ S^1$$ with N_i: number of occurrences of fish species i; P_j: number of occurrences of benthic feature j; S^1 : number of sections sampled.

The ratio of observed over theoretical occurrences ($O_{ij} \ T_{ij}^{-1}$) gives some indication of the preference of the fish for a given benthic feature. However, one should be cautious in the fact that the sections are not independent subunits of a station. Therefore, conclusions from this type of data should stay at a general level and no statistical test was performed.

The species structure of the fish community was studied using multivariate analysis. A Principal Component Analysis (PCA) was performed on the fish densities in order to discriminate characteristic assemblages of species. Species which were found in only one station were not taken into account. Those rare species could not be considered as characteristic of a given bottom type and also introduced too many zeros in the data matrix (Legendre and Legendre, 1984). The fish species which were kept for PCA are listed in table II. Densities were standardized in order to attribute a similar weight to all species.

Table II. - List of the fish species censused. D: density (10^{-2} fish m^{-2}); B: biomass (10^{-2} g m^{-2}); G: groups (A to E) and code of fish kept for the Principal Component Analysis (PCA) (Fig. 5); O: fish which were kept for the PCA but are part of no group. *: fish excluded from the PCA.

Species	D	B	G	Species	D	B	G
MURAENIDAE				**POMACENTRIDAE**			
Gymnothorax sp.	0.01	0.29	*	Abudefduf sexfasciatus	0.03	0.40	
CONGRIDAE				Abudefduf whitleyi	0.02	2.08	*
Muraenesox baggio	-	-	*	Chromis viridis	0.89	2.67	*
SYNODONTIDAE				Chromis fumea	0.24	6.63	C 19
Saurida undosquamis	0.13	15.94	A 1	Dascyllus aruanus	2.94	18.61	*
Synodus binotatus	0.09	8.09	*	Dascyllus trimaculatus	0.11	8.34	*
Synodus dermatogenys	0.02	0.19	*	Neopomacentrotus sp.	0.44	7.91	*
Synodus hoshinonis	0.08	2.44	D 23	Pomacentrus amboinensis	0.02	0.05	*
SCORPAENIDAE				Pomacentrus melanopterus	0.01	0.10	*
Pterois volitans	0.01	0.19	*	Pomacentrus philippinus	0.31	3.22	*
PLATYCEPHALIDAE				Pristotis jerdoni	4.90	1003.5	C 20
onigocia sp.	0.03	1.04	B 9	**LABRIDAE**			
SERRANIDAE				Cheilinus bimaculatus	0.05	0.98	C 21
Pseudanthias sp.	0.22	5.11	*	Cheilinus chlorourus	0.03	1.29	*
Cephalopholis boolack	0.04	2.98	C 13	Halichoeres hoevoni	0.02	0.33	*
Epinephelus cyanopodus	0.04	46.86	E 29	Halichoeres trimaculatus	0.01	0.66	*
Epinephelus maculatus	0.08	5.76	C 14	Suezichthys gracilis	0.06	0.78	C 22
Epinephelus rivulatus	0.01	1.24	*	Thalassoma amblycephalum	0.02	0.39	*
APOGONIDAE				Thalassoma lunare	0.09	2.25	*
Apogon sp.	0.49	2.02	E 30	Thalassoma lutescens	0.01	0.12	*
Apogon catalai	0.04	0.09	*	**SCARIDAE**			
Apogonaureus	0.11	0.89	*	Scarus ghobban	0.10	16.49	*
Apogon fraenatus	0.22	0.67	*	**MUGILOIDIDAE**			
Rhabdamia sp.	2.96	2.96	*	Parapercis sp.	0.09	2.53	A 3
CARANGIDAE				Parapercis cylindrica	0.22	3.94	A 4
Decaptenus nussellii	0.04	2.00	*	Parapercis polyophtalma	-	0.43	*
Gnathanodon speciosus	0.67	71.33	*	**BLENNIIDAE**			
LEIOGNATHIDAE				Petroscirtes breviceps	0.04	0.58	A 5
Leiognathus rivulatus	5.82	1012.7	O 32	**GOBIIDAE**			
Secutor ruconius	5.56	33.33	*	Gobiidae sp.	0.13	2.15	A6
LUTJANIDAE				Amblyeleotris sp.	0.13	0.24	A 7
Lutjanus quinquelineatus	0.17	16.86	C 15	Amblygobius sp.	0.32	4.82	O 33
Lutjanus vittus	0.35	81.09	C 16	Amblygobius bynoensis	0.20	5.40	*
CAESIONIDAE				Amblygobius albimaculatus	0.01	0.20	*
Pterocaesio tile	1.54	45.38	*	Ptereleotris hanae	0.03	0.09	*
GERREIDAE				Valenciennea puellaris	0.03	1.37	*
Gerres ovatus	0.11	7.65	B 10	**SIGANIDAE**			
Gerres sp.	0.04	3.87	*	Siganus canaliculatus	0.04	0.98	*
HAEMULIDAE				Siganus sp.	0.04	1.47	*
Diagramma pictum	0.02	14.85	E 31	**SCOMBRIDAE**			
LETHRINIDAE				Scomberoides commersoni	0.01	45.19	*
Lethrinus genivittatus	4.53	1077.2	D 24	**BOTHIDAE**			
Lethrinus nebulosus	-	1.17	*	Asterorhombus intermedius	0.04	0.53	*
Lethrinus semicinctus	0.01	0.70	*	Engyprosopon grandisquamma	0.01	0.21	B 11
NEMIPTERIDAE				**BALISTIDAE**			
Nemipterus peroni	0.04	1.75	*	Sufflamen chrysopterus	0.01	0.53	*
Scolopsis temporalis	0.10	5.05	A 2	**MONACANTHIDAE**			
MULLIDAE				Paramonacanthus Japonicus	0.03	0.47	A 8
Mulloides flavolineatus	0.02	3.20	*	Pseudalutarius nasicornis	0.16	5.18	D 26
Parupeneus indicus	0.01	0.47	*	**TETRAODONTIDAE**			
Parupeneus heptacanthus	0.01	0.47	*	Arothron hispidus	0.01	0.60	*
Upeneus molluccensis	0.13	7.47	*	Arothron immaculatus	0.15	13.16	O 34
Upeneus tragula	0.38	18.53	C 17	Arothron stellatus	0.04	2.98	*
Upeneus sp.	1.57	70.69	D 25	Canthigaster compressa	0.63	12.42	D 27
CHAETODONTIDAE				Canthigaster valentini	0.05	0.74	D 28
Chaetodon auriga	0.02	0.96	*	Canthigaster sp.	0.03	0.77	*
Heniochus acuminatus	0.06	14.33	C 18	Lagocephalus sceleratus	0.02	1.89	B 12
POMACANTHIDAE				**DIODONTIDAE**			
Centropyge tibicen	0.05	1.84	*	Diodon histrix	-	3.59	*

These standardized values, D, were then transformed into log (D + 1). This procedure is recommended by Legendre and Legendre (1984) in case of over-dispersed data. The bottom type, expressed as the frequency of occurrence on each station of the five sediment categories, and the benthic organisms, expressed as the sum of the abundance estimators (Table I), were used as additional variables. These additional variables were standardized. They do not participate in the analysis but are projected with the fish species and allow to characterize the associations of species.

RESULTS

The fishes
A total of 89 species distributed among 31 families (Table II) were censused. The major species in density and biomass were the leiognathids *Leiognathus rivulatus* and *Secutor ruconius*, the Lethrinidae *Lethrinus genivittatus*, and the Pomacentridae *Pristotis jerdoni* (Table II). The soft bottom fish community of the South Bay of St Vincent had a mean density of 0.44 fish m⁻² (range 0.07-1.03 fish m⁻²) and a mean biomass of 12.7 g m⁻² (range 3.5-27.5 g m⁻²) (Fig. 2). Station 3 stands out as having the most species, the highest density and the largest biomass. In contrast station 1, despite being second in number of species, had the lowest density and biomass.

The trophic structure is given in Figure 3. The number of species was significantly different between trophic categories (χ^2 test, $\alpha < 0.01$), macro-carnivores having significantly more species than the other groups. Density and biomass were also significantly different between the various trophic groups (Anova, $\alpha < 0.001$). A multiple comparison among means was then performed using a Tukey's standardized range test (Sokal and Rohlf, 1981). This test indicated the presence of two groups: a group of high density and biomass composed of macro-invertebrate feeders and planktivores, a second group with lower densities and biomasses represented by the piscivores, micro-invertebrate feeders and herbivores.

The benthos
The various types of sand covered 82 % of all stations, silt being found only at stations 6 and 10 (Table III), where few species of invertebrates were seen (Table IV). Species richness and abundance of the invertebrates were highest at stations 1, 3, 4 and 11. On all four of these stations weak water currents were reported during the dives. These stations supported also the most cnidarians. Algae, with the exception of station 4, were located either in the middle of the bay (stations 3, 8, 9) or in the Northwest part (station 1, 2, 11).

Correlations between fish and benthos
A systematic search for correlations was performed between the species richness, the density and the biomass of fishes, and the species richness and the abundance estimates of the benthic organisms (Table V). Only three correlations were significant ($\alpha < 0.05$). The number of fish species was correlated with the species richness and the abundance of cnidarians. Fish density was significantly correlated with the sponges and ascidian abundance. Piscivores were correlated to most benthic organisms except plants whereas the other trophic groups were correlated to only one or two benthos groups (Table V).
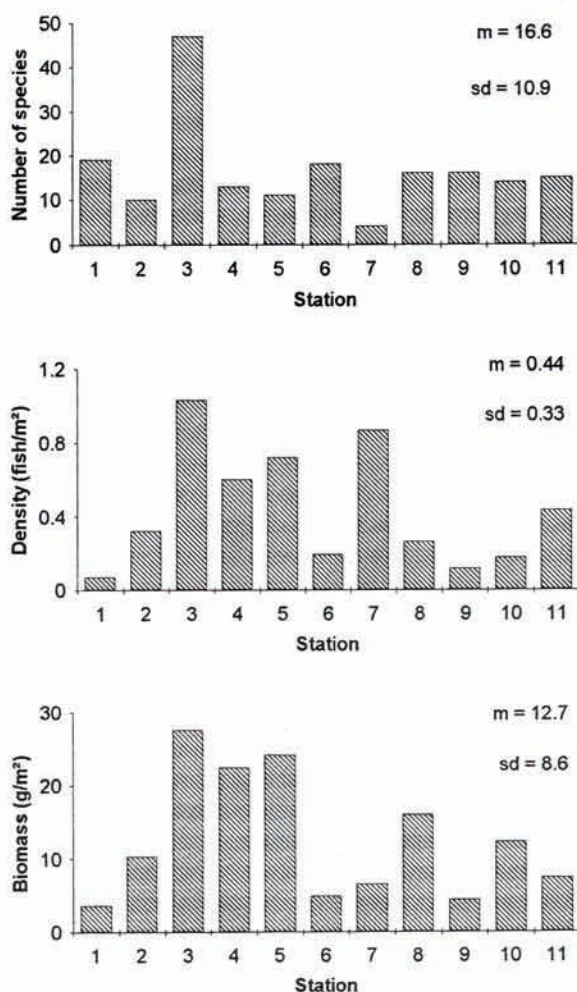
Fig. 2. - Number of fish species, density and biomass estimated for each station. m: mean; sd: standard deviation.

Fish species associations and their relation to the benthos

Station 3, which combined the most species of fish and benthic organisms, appears separated along axis 1 of the PCA, and stations 6 and 10, which were the only ones with silt, are separated on the lower part of axis 2 (Fig. 4). Station 1 was atypical in having a high benthos species richness but the lowest fish density. These projections together with the projection of the additional variables (Fig. 5) show that the axis 1 is an indicator of the benthos species richness and axis 2 an indicator of siltation.

Five fish species groups (A-E) were defined (Fig. 5, Table II). Group A corresponds to fishes living in silted areas with no or few large benthic organisms. The species of group

Number of species
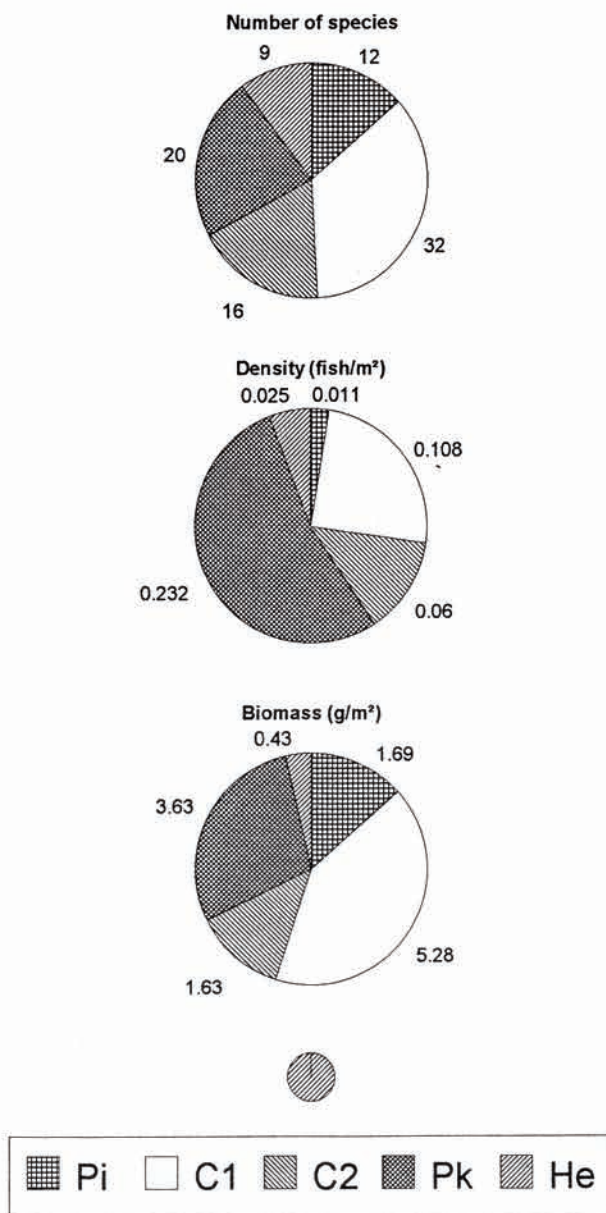

Density (fish/m²)

Biomass (g/m²)

Fig. 3. - Overall trophic structure of the fish community (mean of all stations). Pi: piscivores; C1: macro-invertebrate feeders; C2: micro-invertebrate feeders; Pk: plankton feeders; He: herbivores.

A are known to occur in similar habitats, with the exception of *Petroscirtes breviceps* which is usually found on *Sargassum* algae (Table VI). The preference of these species for silt was confirmed by the ratio of the observed over the theoretical distribution of the spe-

Table III. - Frequency (%) of the various bottom types among the stations.

Bottom type	Station number											Total
	1	2	3	4	5	6	7	8	9	10	11	
Sand	100		100									18
Silted sand		100		100	30		5	90	100			39
Silted sand with debris					70		95	10			100	25
Silt						60				80		13
Silt with debris						40				20		5

Table IV. - Species numbers and abundance of benthic organisms. N: number of species; A: sum of the abundance estimators for a given group of organisms.

Organisms		Stations										
		1	2	3	4	5	6	7	8	9	10	11
Plants	N	6	5	1	1	2	0	5	4	4	1	5
	A	25	50	80	1	9	0	11	20	20	1	67
Echinoderms												
Holothurians	N	2	5	6	7	4	3	4	4	3	2	1
	A	4	30	29	15	27	10	10	13	7	33	30
Urchins and starfishes	N	4	1	3	3	1	2	3	7	2	0	3
	A	83	8	3	34	1	2	5	17	4	0	12
Ophiurids and crinoids	N	0	0	1	3	0	0	0	0	0	0	1
	A	0	0	1	7	0	0	0	0	0	0	8
Total	N	6	6	9	13	5	5	7	11	5	2	5
	A	87	38	32	56	28	12	15	30	11	33	50
Sponges ascidians	N	3	3	6	9	3	3	2	3	3	1	3
	A	19	14	103	63	91	12	38	14	7	1	19
Cnidarians												
Actinians	N	1	0	0	1	0	0	0	0	1	0	1
	A	1	0	0	1	0	0	0	0	1	0	3
Alcyonarians	N	1	0	2	2	0	2	0	0	0	0	3
	A	1	0	33	9	0	11	0	0	0	0	12
Corals	N	3	3	7	2	1	1	2	3	3	1	4
	A	88	3	111	11	8	30	11	14	14	8	44
Stylaster	N	0	0	0	1	0	1	0	1	0	0	1
	A	0	0	0	1	0	3	0	3	0	0	3
Gorgonians and Antipatharia	N	0	0	0	1	0	1	0	0	0	0	0
	A	0	0	0	1	0	1	0	0	0	0	0
Total	N	5	3	9	7	1	5	2	4	4	1	9
	A	90	3	144	23	8	45	11	17	15	8	62
Molluscs and worms	N	3	1	2	8	3	3	2	3	3	2	1
	A	32	8	31	123	36	63	38	9	10	2	30
Total	N	23	18	28	38	14	16	18	25	20	7	23
	A	253	113	390	266	172	131	113	90	63	45	228

Table V. - Correlations (Spearman's coefficient) between fish and benthos. N: number of species; D: density; B: biomass; A: abundance; Pi: piscivores; C1: macro-invertebrate feeders; C2: micro-invertebrate feeders; Pk: plankton feeders; He: herbivores; +: $\alpha < 0.10$; *: $\alpha < 0.05$; **: $\alpha < 0.01$.

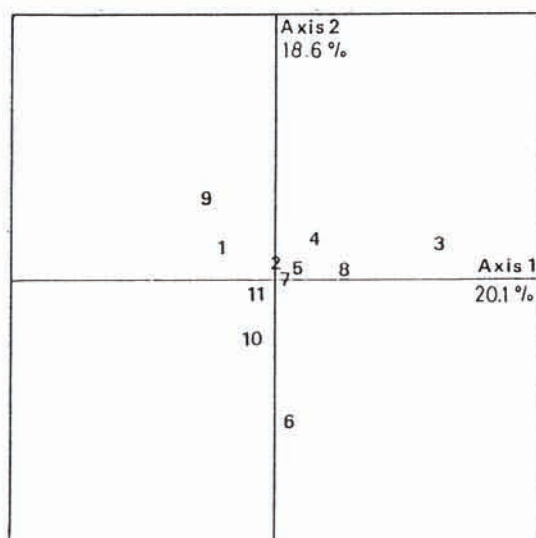|		All fish			Pi			C1			C2			Pk			Gr		
		N	D	B	N	D	B	N	D	B	N	D	B	N	D	B	N	D	B
All benthos	N				+	+	**	+				*							
	A				*	*													
Plants	N									*							+		
	A																		
Echinoderms	N																		
	A				*	+					+								
Sponges-ascidians	N				+	**	*												
	A	**	+			+								*	*				
Cnidarians	N	*			**		*					*		*					
	A	**			**	**		*				*		+					

Fig. 4. - Projection of the stations on the first two axes determined by the Principal Component Analysis. The percentage of the explained variation is given for each axis.

cies (Table VII). However, *Parapercis cylindrica* was found preferentially with free corals (*Cycloseris cyclolites* and *Trachyphyllia geoffroyi*). Species of group B were found on bare sand. This tendency is confirmed by the ratio of table VII. These species were usually reported on muddy rather than sandy bottoms (Table VI). Group C is constituted by fish associated to rich benthic fauna (Table VII). Most of the fishes in this group were usually associated with reefs or coral (Table VI). In St Vincent Bay these species were often but not always related to coral (Table VII). In particular, they all show a preference for sponges (except *Cephalopholis boenack*) and sand. Group D fishes were found on what is known in
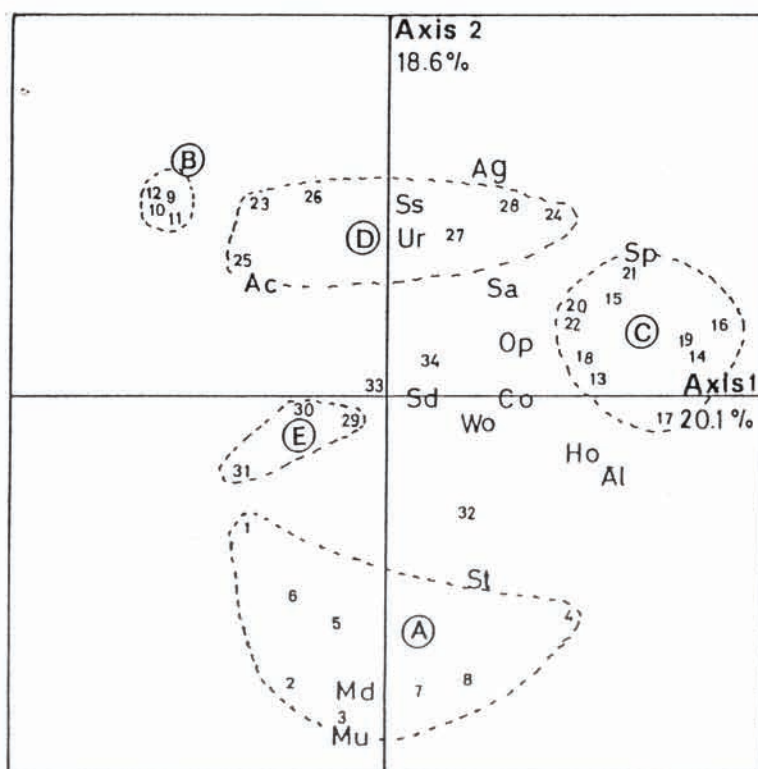
Fig. 5. - Projection of the fish species and the additional variables on the first two axes determined by the Principal Component Analysis. The percentage of the explained variation is given for each axis. See table II for species codes. Sa: sand; Ss: silted sand; Sd: silted sand with debris; Mu: silt; Md: silt with debris; Ag: algae; Sp: sponges; Co: corals; Al: alcyonarians; Ac: actiniarians; St: stylasters; Wo: worms; Ur: sea urchins; Ho: holothurians; Op: ophiurids and crinoids.

New-Caledonia as "grey bottoms" (Chardy *et al.*, 1988) which is usually silted sand with *Halimeda* algae. This preference for sand is indicated by the ratio of table VII, but no particular association of these fishes with algae was reported. These fishes were also linked to the presence of the worm *Eunice tubifex* (Table VII). There is not much data available on the habitat of these species (Table VI). *Canthigaster valentini* was not usually recorded on this type of habitat but was rather found associated with corals and reefs. Group E is composed of three species which were often encountered together in crevices of bed rock. This type of habitat was found on three occasions during the survey but on different substrata. *Diagramma pictum* and *Epinephelus cyanopodus* were most often associated with isolated coral reefs (Table VI). This group was found preferentially on sand with debris, or silt with debris, together with algae (Table VII). *Leiognathus rivulatus* appears in none of the groups; it is a species which schools at times near the bottom but also migrates in the water column to feed on plankton. It is therefore not directly correlated with benthic organisms and may be found over a number of substrata.

Table VI. - Review of the bottom type from which the main species of groups A-E have been reported. 1: Allen (1975); 2: Allen (1985); 3: Allen and Randall (1977); 4: Allen and Swainston (1992); 5: Bell *et al.* (1984); 6: Blaber and Blaber (1980); 7: Fisher and Bianchi (1984); 8: Fourmanoir and Laboute (1976); 9: Gomez *et al.* (1988); 10: Grant (1978); 11: Hilomen and Gomez (1988); 12: Kulbicki *et al.* (1990); 13: Loubens (1978); 14: Marchal *et al.* (1981); 15: Masuda *et al.* (1984); 16: Munro (1967); 17: Myers (1989); 18: Randall and Heemstra (1991); 19: Smith and Heemstra (1986); 20: Stephenson *et al.* (1982).

Species	Bottom type
Group A	
Saurida undosquamis	mud[7 20], sandy bottom[15],
Scolopsis temporalis	coastal waters[16]
Petrosirtes breviceps	sandy areas with sargassum[17], sargassum and other, seaweeds[15]
Paramonacanthus japonicus	mud[20], coastal waters[16]
Group B	
Gerres ovatus	sandy mud[20], estuaries with mud[6], mangrove creek[5]
Engyprosopon grandisquamma	shallow muddy and sandy bottoms[7], sand and clay bottoms[10]
Lagocephalus sceleratus	sand with shells and silty sand[14]
Group C	
Cephalopholis boenack	coral and rock, rich areas in sheltered turbid lagoon reefs[17], around coral reefs[15] dead reefs in sheltered areas[19]
Epinephelus maculatus	juvenile in shallow coral rubble, adult on isolated coral heads[17]
Lutjanus quinquelineatus	shallow coral reefs[7], *Acropora* [8], sheltered lagoons[2]
Lutjanus vittus	flat bottom with scattered coral outcrops[17], rocky and coral reef areas[7,.2]
Upeneus tragula	sandy to muddy bottoms[17], sand or silty sand near coral reefs[7], shallow algae bedds[8]
Heniochus acuminatus	protected lagoons[17]
Chromis fumea	reef slopes[15], isolated patch reefs on sandy bottoms[12]
Pristotis jerdoni	flat sandy bottoms[1]
Cheilinus bimaculatus	rubble or clumps of algae in "dead" areas[17], seagrass beds[19]
Group D	
Lethrinus genivittatus	silty sand with algae[8], silted sand near coast[13]
Canthigaster compressa	clear and sandy bottom[17], wharf pilings in silty harbours[3]
Canthigaster valentini	coral heads, seaward reefs[17], dead coral with algal covering[9], sheltered areas[11]
Group E	
Epinephelus cyanopodus	isolated coral heads of lagoons[17,18] isolated coral bommies in sandy areas[4]
Diagramma pictum	sandy to muddy bottom close to patch reefs[17], around coral[19], sandy areas of coral reef lagoons[10]

In groups A and B most fishes are small macro-invertebrate feeders (*Gerres ovatus, Scolopsis temporalis, Parapercis* spp., Gobiidae spp., *Engyprosopon grandisquamma*) and micro-invertebrate feeders (*Gerres ovatus,* Gobiidae spp., *Amblyeleotris* sp.), the only other

Table VII. - Ratio of the observed frequencies over the theoretical frequencies of the main fish species for the main substrata. See material and methods for explanations. Sa: sand; S. sa: silted sand; Sa de: sand and debris; Si: silt; Si de: silt and debris; Spon: sponges; Alcy: alcyonarians; *E. tub*: *Eunice tubifex* (worm); nó symbol: ratio < 1. *: 1 < ratio < 2; **: 2 < ratio < 10; ***: 10 < ratio.

Species	Sa	S. sa	Sa de	Si	Si de	Algae	Spon	Alcy coral	Free coral	E. tub
Group A										
Saurida undosquamis				**	**					
Scolopsis temporalis				*	***					
Parapercis cylindrica	**				**		*	*	***	
Petroscirtes breviceps		*			**		*	*		
Gobiidae spp.				**	**					
Amblyeleotris sp.				**	**					
Paramonacanthus japonicus	**				**		**			
Group B										
Onigocia sp.	**	*				*				
Gerres ovatus	*	*								
Engyprosopon grandisquamma	**	*				*				
Lagocephalus sceleratus	**	*								
Group C										
Cephalopholis boenack	**				***		**			
Epinephelus maculatus	*						**		***	*
Lutjanus quinquelineatus	**				*	*	**			
Lutjanus vittus	***				*	*	**	***	***	
Upeneus tragula	*	*					*		**	**
Heniochus acuminatus	**					*	*	**		
Chromis fumea	**				***		*			
Pristotis jerdoni		**			*		**			**
Suezichthys gracilis	*					**	*			
Cheilinus bimaculatus	**	*					**		***	**
Group D										
Synodus hoshinonis		*	*			*	*			*
Lethrinus genivittatus	**	*					**	*	**	**
Upeneus sp.	**	*								
Pseudalutarius nasicornis	**	*					*			**
Canthigaster compressa	*	*				*	*		**	*
Canthigaster valentini	**				**		*		***	
Group E										
Epinephelus cyanopodus			**			**	*			
Diagramma pictum	*		*		***	*				
Apogon spp.	**		**			*	*			

trophic group being piscivores represented by *Saurida undosquamis* and *Onigocia* sp. Group C is characterized by plankton feeders such as *Chromis fumea* and *Pristotis jerdoni*. Macro-invertebrate feeders such as the small labrids, *Cheilinus bimaculatus* and *Suezichthys gracilis*, and larger lutjanids, *Lutjanus quinquelineatus* and *Lutjanus vittus*, are the second main component of group C. The fishes from group C were usually found on hard substrata, near coral formations or very large sponges which seem to be used as refuges. Group D is characterized by macro-invertebrate feeders of small to medium size, such as *Lethrinus genivittatus* and *Upeneus* sp., and also by small micro-invertebrate feeders such as *Canthigaster compressa, Canthigaster valentini* and *Pseudalutarius nasicornis. Canthigaster compressa* and *Pseudalutarius nasicornis* are well adapted to camouflage among algae such as the *Halimeda* and the *Sargassum* which are commonly found on "grey bottoms" (Chardy *et al.*, 1988).

DISCUSSION

The fish species composition and the trophic structure observed during this study are closely related to the results of an exploratory trawl survey from the same grounds (Kulbicki and Wantiez, 1990a), indicating that the sampling procedure was satisfactory. Previous trawling has indicated the presence of 191 species in the South Bay of St Vincent. In that latter study 40 species can be considered as important, being present in more than 25% of the hauls. Only 9 of these 40 species were not recorded in the present survey. These species are either cryptic (*Saurida gracilis, Inimicus didactylus, Synchiropus rameus*) or schooling species (*Leiognathus bindus, Leiognathus leuciscus, Leiognathus splendens, Sphyraena putnamie*). Two species, namely *Lactoria cornuta* and *Tetrasoma gibbosus*, usually were easily detected along transects. A number of species which had not been previously taken during the experimental trawling were also censused in the present study. These are mainly reef fishes such as *Centropyge tibicen, Abudefduf sexfasciatus, Abudefduf whitleyi, Halichoeres hoeveni, Halichoeres trimaculatus* and *Thalassoma lutescens*, or burrowing species such as *Amblygobius albimaculatus, Amblygobius bynoensis* and *Valenciennea puellaris*. The trophic structure found during this diving survey is not significantly different in either density or biomass from what was observed during a trawl survey over the same area (Kulbicki and Wantiez, 1990a; Wantiez, 1993, 1994). There are however some differences between the two surveys at the species level. Thus, in the present study there were no large piscivores, such as large groupers (Serranidae) or barracudas, no clupeiforms among the plankton feeders, and the largest macro-invertebrate feeders such as Lutjanidae and Lethrinidae were seen only in small numbers. Diving was better than trawling because of the more precise nature of the information which can be obtained simultaneously on fishes and benthos. Kulbicki and Wantiez (1990b) have found that trawls underestimated actual densities for several fish species sampled in this type of fishery. Moreover, small species such as *Chromis fumea* (group C), *Parapercis cylindrica* (group A) and most Apogonidae (group E) are absent from the trawls because of their small size. These species may be important in the community and disturbance of their populations by trawls, not directly revealed by the analysis of trawl catches, may have important indirect effects on commercial species.

Correlations between the fish community and the benthos characteristics, similar to those observed during this study, have also been observed among coral reef fishes of the

Chesterfield islands (Kulbicki *et al.*, 1990). Fish diversity was also correlated with cnidarian diversity and abundance. Such a relationship is frequently observed on coral reefs (Hobson, 1974; Reese, 1977; Harmelin-Vivien and Bouchon-Navarro, 1983; Galzin, 1987; Kulbicki *et al.*, 1990). At a larger spatial scale, the species richness of the ichthyofauna was linked to the species diversity and the abundance of the benthos in the wide open North Lagoon of New Caledonia, the characteristics of which vary greatly in space (Wantiez, 1993). Species associations determined in the North Lagoon were also determined by two gradients, one linked to siltation and the other to benthos diversity and abundance (Wantiez, 1993). Species occurring where the benthos was diversified and abundant were contrasted to species occurring where the benthic assemblages were scarce. Similar abundant species were globally characteristic of similar environments in the two studies (*Saurida undosquamis* and *Scolopsis temporalis* on one hand, and *Lethrinus genivittatus*, *Upeneus* sp. and *Canthigaster compressa* on the other hand). This suggests that the structural organisation of soft bottom fish communities is likely to be the same in all New Caledonian lagoons. Similar patterns of distribution have been found in Queensland (Australia) (Cannon *et al.*, 1987; Watson and Goeden, 1989; Watson *et al.*, 1990).

The links between species distribution and benthos characteristics have several consequences for trophic structure. Micro-invertebrate feeders were negatively correlated to cnidarians and to benthic organisms in general. This can be explained by the fact that these fishes feed mainly on prey which are found in silted areas where conspicuous macrobenthic organisms are scarce. The relationship between plankton feeders and sponges is due to concentrations of the damselfish *Pristotis jerdoni* over large black sponges (genus *Ircinia*) that could be explained by a plankton input. A similar relationship was found by Kulbicki *et al.* (1990) in the Chesterfield islands between plankton feeding damselfishes and filtering organisms such as sponges and ascidians. The absence of relationship between herbivores and the benthos is likely to be due to the fact that this trophic group was always scarce (1 species per station, 0.004 fish m^{-2} and 0.076 g m^{-2}) with the exception of station 3 (7 species, 0.23 fish m^{-2} and 3.8 g m^{-2}). This was also the station with the highest plant cover and the largest benthos abundance.

Comparison of the species composition with the catch composition in the prawn trawl fishery of Queensland (Jones and Derbyshire, 1988) shows that 21 species were common representing 28 % of the 75 taxa identified at the species level. A similar comparison with trawl catches from the Arafura Sea (Indonesia) and the Gulf of Carpentaria (Australia) (Okera and Gunn, 1986) indicated 23 species in common. Among the species which characterize a group in the present study, *Saurida undosquamis*, *Epinephelus cyanopodus*, *Epinephelus maculatus*, *Lutjanus vittus*, *Diagramma pictum*, *Lethrinus genivittatus*, *Upeneus tragula*, *Engyprosopon grandisquamma*, *Paramonacanthus japonicus*, *Pseudalutarius nasicornis* and *Lagocephalus sceleratus* are either commercially important or abundant in the catch of most soft bottom trawl fisheries in the tropical Indo-Pacific. The catch composition of these fisheries fluctuates with time and it is thought that these changes are in part due to the destruction or modification of the benthic communities by the trawl (Sainsbury, 1982; Hutchings, 1990; Harris and Poiner, 1991). Such changes may induce increase of some less desirable species. Thus *Saurida undosquamis* replaced *Merluccius merluccius* in Israel after the start of trawling (Ben-Yami and Glaser, 1973). The same species increased significantly in the trawl fisheries of the NW Australian shelf (Sainsbury, 1982), a second species of *Saurida* also becoming important whereas it was almost absent at the start of the fishery. Caveriviere *et al.* (1981) indicate the proliferation

of *Balistes carolinensis* on the coast of Western Africa. One of the possible explanations of this sudden increase is the development of a shrimp fishery in the same area and the decrease of the clupeid *Brachydeuterus auritus*. In the present case, two Monacanthidae, *Paramonacanthus japonicus* and *Pseudalutarius nasicornis* could present the same potential for sudden increase. The impoverishment of the benthic communities caused by trawling could favour species of the group A and B, whereas fishes of the groups C, D, E might be detrimentally affected. On the NW shelf of Australia Lutjanidae, in particular *Lutjanus vittus*, were found preferentially on bottoms with dense benthos, and this family has declined in the catch as a result of the alteration of the habitat by trawling (Sainsbury, 1982). In St Vincent Bay data from a monthly trawl survey over one year suggests that *Lutjanus vittus* is particularly sensitive to this problem (Wantiez, 1993). Another aspect of trawling is the destruction of juveniles. In the present study three species, *Diagramma pictum* (group E), *Epinephelus maculatus* (group C) and *Lagocephalus sceleratus* (group B) were mainly found as juveniles. These three species are fished as adults along the barrier reef and in the untrawlable parts of the lagoon (Kulbicki *et al.*, 1987). If a trawl fishery developed in St Vincent Bay one would expect to see in the nearby lagoon a decrease of *Diagramma pictum* and *Epinephelus maculatus* and maybe an increase of *Lagocephalus sceleratus*. The first two species are economically important whereas the latter one is a nuisance to line fishing and has no commercial value.

This study confirms statistical associations between the fish community and benthic characteristics, and supports the hypothesis explaining the declines in Northwest Australia and Southeast Asia trawling grounds (Sainsbury, 1982; Hutchings, 1990; Harris and Poiner, 1991). Modification of the environment may induce important ecological changes in the species structure and the trophic organisation of the fish communities, by reducing ecological niches through diminution of benthic complexity (decrease of megabenthic formations such as corals and sponges).

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